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ORIGINAL ARTICLE

Phenological behavior and floral visitors of *Pentaclethra macroloba*, a hyperdominant tree in the Brazilian Amazon River estuary

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Abstract

Key Message **Amazon River tide is an environmental drive that stimulates *Pentaclethra macroloba* to disperse its seeds during the flood peak. Reproductive strategies of the species result in its dominance in the Amazon.**

Abstract Natural history of hyperdominant tree populations in the Brazilian Amazon Region is still unknown in plant science. *Pentaclethra macroloba* (Willd.) Kuntze (Fabaceae) is a hyperdominant tree species which has multiple uses and its seeds are extensively explored to extract medicinal oil. We evaluated the phenological cycles and floral visitors of *P. macroloba* and the effect of the daily tide of the Amazon River on the phenophases. Phenophases of flower bud, anthesis flowers, immature fruit, ripe fruit, seed dispersal, new leaf, mature leaf, and leaf fall of 29 trees in the Northeast of the Brazilian Amazon were monitored during 28 months. Hydrometeorological data of rainfall, maximum temperature and flood height on the tree trunk were obtained. Generalized Linear Models were used to explain the relationship between phenophases and hydrometeorological parameters. Flowering was synchronized in the dry season (flower buds: $\beta_{temperature} = 1.30$, $p < 0.01$ and flowers in anthesis: $\beta_{temperature} = 1.84$; $p < 0.001$). Immature fruits appeared during the dry season ($\beta_{temperature} = 0.67$; $p < 0.01$) and ripe fruits in the rainy season. Seeds were dispersed during the rainfall ($\beta_{rainfall} = 0.0051$; $p < 0.01$) and flooding of the river ($\beta_{water} = 0.12$; $p < 0.001$). There was no relationship between leaf change and hydrometeorological variables. The main floral visitors were wasps, bees and ants. The rainfall seasonality is a key factor that stimulates reproductive events of *P. macroloba.* Daily river flooding can be considered a driver that stimulates the tree to disperse its seeds at the peak of the river flood, where they can be transported the long distances.

Keywords Daily tide · Phenophases · Pollination · Pracaxi oil · Rainfall · Reproductive strategy.

Introduction

Phenology study the interactions of seasonal biological events with the abiotic and biotic factors of the habitat (Lieth 1974). Environmental triggers that stimulate and drive the phenological patterns of tropical trees are still very much questioned and debated by plant ecologists (Morellato et al. 2013; Mendoza et al. 2017). The great diversity of phenological patterns found in tropical forests may be the result of a long evolutionary process of adaptation to changes in the environment and to dispersing and pollinating agents (van Schaik et al. 1993; Sakai 2001).

In the flooded forests of the Amazon Region, the elevation and descent of the water level of the Amazonian rivers is a phenomenon known as "flood pulse" (Junk 2001). Flood pulse is the main driver of the phenological patterns of flooded forests (Schöngart et al. 2002; Haugaasen and Peres 2005; Parolin et al. 2010) and it also acts as an environmental filter selecting species adapted to the constantly flooded environment (Luize et al. 2018). The floodplain forests of the Amazon estuary are bathed by the Amazon River and comprises an area of approximately 199,281 km^2 (Junk and Piedade 2010), between the coastal areas of the States of Amapá and Pará in Brazil. Different from the Central

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Amazonia, where the flood pulse is monomodal and conditions the species to long periods of flooding that can last up to 243 days and reach a mean height of 6 m by the river water mark registered on the tree trunks (Schöngart et al. 2002), the Amazon estuary is influenced by ocean tides, resulting in two daily flood cycles (Junk et al. 2014), that can reach a height of up to 4 m in the rainy season (Cunha et al. 2017).

The flood pulse of the Central Amazon floodplains is the main driver that models reproductive cycles (Parolin et al. 2010) and phenological patterns of the trees (Worbes 1997; Schöngart et al. 2002; Haugaasen and Peres 2005; Ferreira and Parolin 2007; Hawes and Peres 2016). However, the influence of the tidal cycles on the phenology of the trees in the Amazon estuary, where the flood pulse is polymodal and of low amplitude (Junk et al. 2014), is still little known (Cattanio et al. 2004; Dantas et al. 2016).

Sedimentary material of Andean and pre-Andean origin (Wittmann et al. 2010) deposited inside the forest by the Amazon River, and the annual flood cycles, allows the establishment of several tree species adapted to the daily flood cycle (Carim et al. 2016). One of these species is *Pentaclethra macroloba* (Willd.) Kuntze, locally known as pracaxizeiro, which is a hyperdominant Fabaceae from the Amazon region (ter Steege et al. 2013) and has high frequency in the Amazon estuary (Carim et al. 2016). *P. macroloba* is a pioneer species, monoecious (Barros et al. 2017), with height of 13 m and diameter of 26 cm means, bipinnate leaves, inflorescence presents up to 411 flowers, dry legume fruit has explosive dehiscence and the flattened brown seed has an air pocket between the cotyledons which facilitates hydrochoric dispersion (Dantas et al. 2021). *P. macroloba* forms highly aggregate populations (Dantas et al. 2017) and it is adapted to the daily tide of the Amazon River, presenting adventitious roots and lenticels to increase respiratory efficiency in conditions of low oxygen availability in the rhizosphere (Dantas et al. 2021).

Hartshorn (1983) considers the existence of three large populations of *P. macroloba* in Latin America. The first population, widely studied, is concentrated in Costa Rica, mainly in the La Selva Forest Reserve, where it has population monodominance. The second population is concentrated in the extension from Panama to Colombia. The third and last population is located in the Northeast of the Brazilian Amazon and its natural history is little known.

Pentaclethra macroloba has great socioeconomic relevance in the Amapá State. Many riverside women collect the seeds to extract the oil, a traditional knowledge that is passed from generation to generation. The oil is usually sold at traditional fairs and even for some cosmetic industries. The oil is also used by riverine forest people as a natural medicine, due to be a powerful healing agent for wounds and burns (Banov et al. 2014). The bark of the *P. macroloba* trunk has triterpenoid saponins that act against hemorrhage caused by the venom of *Bothrops* genus vipers (Silva et al. 2007).

Multiple uses of *P. macroloba* and the low knowledge about basic aspects of its ecology are factors that make the species vulnerable to overexploitation and the exhaustion of its natural resources, mainly the seeds, in the Amazon estuary. Therefore, phenological studies of *P. macroloba* are essential to elucidate the seasonal growth and reproduction rhythms of trees, related to the abiotic and biotic characteristics of the habitat (Lieth 1974). One of the objectives of the phenological studies is to evaluate the rhythm of flowering (emission of flowers and floral development), fruiting (fruit ripening and seed dispersal) and leaf change (emission of new leaves and leaf senescence) phases (Alencar 1998). What is known about the phenology of *P. macroloba* is that it has annual pattern of flowering and fruiting and remains with its canopy evergreen (Freitas et al. 2003; Vilchez et al. 2007). These few studies are at the community level and superficial, being that a large knowledge gap remains unanswered about the interactions of the phenological phases of the species with its habitat.

Plant–pollinator interactions play an important role in diversification of the flowering patterns of tropical trees (Oliveira and Rech 2018). The periodicity and intensity of the flowering are factors directly related to attractiveness and availability of floral resources for the pollinators (Vieira et al. 2012). Many trees show synchronized flowering (Augspurger 1983) and floral adaptations (Fouks and Wagoner 2019) to attract pollinators. This synchrony is certainly adaptive, as many tree species, such as *P. macroloba*, invest enough energy in floral development, which can last for days, only then to expose their reproductive organs for 1 or 2 days.

We aimed to determine the reproductive and vegetative phenophases pattern and evaluate the main floral visitors of *P. macroloba* to assist in the management and conservation of its natural resources in the Amazon estuary. Due to its high adaptation and dominance in the Amazon estuary, we expect a high synchronization of the phenological events of *P. macroloba* with the flood pulse of the Amazon River.

Materials and methods

Study area

Phenological monitoring was conducted in the Fazendinha Environmental Protection Area (APA), with authorization of the Amapá State Environmental Secretariat, environmental authority responsible by the APA (Supplementary 1). This area is located in the Macapá city (Fig. 1), in the Southeastern region of the Amapá State, Brazil (00° 03′ 04.24″

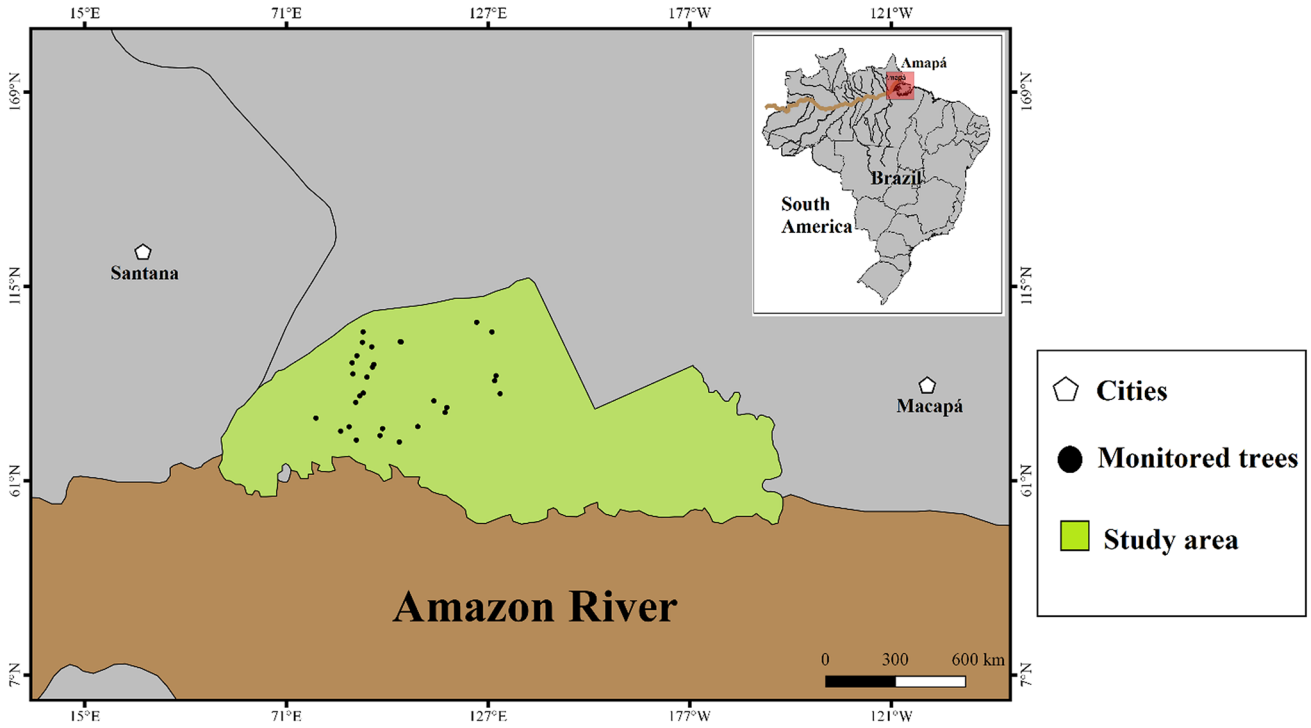

Fig. 1 Fazendinha Environmental Protection Area (APA) in the floodplain forest of the Amazon estuary, Macapá, Brazil

S and 51° 07′ 42.72″ W). This area has 136.59 ha of forest periodically flooded by the Amazon River.

The climate condition in the region is of the Am type, rainy tropical (Alvares et al. 2013). In the Amapá State, the rainy period starts in December, with the concentration of rainfall in March, when the peak of rainfall remains above 60 mm/month until August. The drought period starts in September when the rainfall is below 60 mm monthly. Climatological data from 1987 to 2016 show that the mean annual rainfall is 2460 mm and the mean maximum temperature varies from 30° to 32 °C (Vilhena et al. 2018).

The soils of the estuarine floodplain forests are classified as typical Melanic Gleysols Ta Eutrophic, with predominance of silt. Both the sediment and the soil are formed by smectite, illite, kaolinite, goethite, anatase and quartz (Pinto 2014).

Vegetation is classified as Dense Alluvial Ombrophilous Forest (IBGE 2012) and evergreen, with dominance, among trees, of *Mora paraensis* (Ducke) Ducke, *Astrocaryum murumuru* Mart., *Pentaclethra macroloba* (Willd.) Kuntze, *Carapa guianensis* Aubl. and *Virola surinamensis* (Rol.) Warb. (Carim et al. 2016).

Phenological data and floral visitors

An inventory of all individuals with Diameter at Breast Height DBH ≥ 5 cm conducted in the study area registered 2072 trees. Twenty-nine adult and productive trees of different diametric classes (with diameters between 14 and 49 cm measured at a height of 1.30 m from the ground) and dominant and codominant in the canopy (between 15 and 30 m of height) were selected for phenological observations and to record the activity of floral visitors. Morellato et al. (2010b) recommend sampling at least 15 individuals to represent the phenological pattern of the population. The selection criteria were good phytosanitary aspect and minimum distance of 50 m between individuals. The species was identified and the vouchers were deposited in the Embrapa Herbarium Amazônia Oriental—IAN (registration numbers IAN192676 and IAN192677) (Dantas et al. 2021).

Phenological monitoring was conducted from September 2017 to December 2019, fortnightly, totaling 28 months of observations. In this study, we consider as: flowering—the emission of the floral bud until the senescence of the flower, fruiting—emission of the fruit until the dispersion of the seed and leaf change—the emission of leaf buds on the branch until the senescence of the leaf.

The phenophases observed were: (1) flower buds, begins when the species has small green closed buds and ends with the opening of the corolla; (2) flowers in anthesis, begins with the opening of the corolla and ends when staminodes lose their white color, changing to a brown color until their complete senescence; (3) immature fruits, begins when small pods of light green color appear with shiny surface and

ends when the pods acquire dark green color and obtain over time brown color; (4) ripe fruits, when the fruits have brown color and become dry; (5) seed dispersal, occurs when the dried fruit releases the seeds—autochoric dispersion; (6) new leaves, begins when the branches produce small leaves of violet color, changing to a light green color, and ends when the leaves have dark green color; (7) mature leaves, when the leaves lose their dark green color and change to brown color until leaf senescence; and (8) leaf fall, disconnection of the petiole leaf from the branch, causing empty spaces in the crown. The trees were monitored with the aid of binoculars (60 × magnification).

Phenophases were semi-quantified using the methodology proposed by Fournier (1974), in which the phenological events are grouped into four categories of 25% amplitude. The frequency of manifestation of the reproductive phenophases was classified as: continual, sub-annual, annual and supra-annual (Newstrom et al. 1994). The pattern of production and leaf fall were determined based on three categories: deciduous, brevi-deciduous and evergreen (Schöngart et al. 2002).

Thirty-one inflorescences of 15 individuals were marked and monitored, from August to November 2018 every 2 days, to assess the stages of floral development over time and the floral longevity of *P. macroloba*. Ninety flowers were marked to estimate floral longevity. Floral longevity was considered from floral anthesis to flower senescence (Primack 1985).

The behavior and frequency of floral visitors were monitored during August to November 2018, every 2 days, in ten trees. Focal observations were conducted, in each tree, in the morning (5 h) and afternoon (5 h) period (Malucelli et al. 2018). The behavior of the floral visitors was filmed with camera of high-resolution (Sony HDR-CX405 60 ×), for a better analysis of the visitor-flower interactions. Insect floral visitors were captured with the aid of traps, 1.5 L polyethylene bottle with inverted funnel, containing a sugary solution (water + sugar) (PPBio 2019). The traps were placed close of the monitored inflorescences, at heights of 15–25 m in the tree crowns. The parameters analyzed of the floral visitors were: frequency of visits, foraging duration and number of visitors per inflorescence. The insects were identified and deposited in the entomological collection of the National Research Institute for Amazon.

Hydrometeorological data

Monthly data of maximum temperature (°C) and accumulated precipitation (mm) were obtained from the Macapá Climatological Station (00°02′07′′ S e 51°05′55′′ W), located about 1 km from the study area (INMET 2019).

The height of the flood was monitored inside the forest together with the phenological observations. For this, white strings were installed parallel, at a height of 1 m, on the trunk of each monitored tree. The Amazon River water, rich in sediment, stains the white string and records a brownish mark, facilitating the measurement of the height that the water reaches with a tape measure. Every fortnight, the strings were changed for subsequent evaluation. In addition, tide level data of the Amazon River was obtained from the Porto de Santana Maregraph Station (00° 03′ 07″ S and 51°10′ 1 W), about 6 km from the study area (CHM 2019).

Data analysis

To obtain a single response value, the fortnightly data of each phenophases were converted to monthly data through the sum of the fortnightly phenological data, divided by the number of observations in the month for each individual. The intensity of each phenophase in the species was determined using the Fournier formula (Fournier 1974):

$$\% \text{ Fournier} = \frac{\sum \text{Fournier}}{4 \times N} \times 100$$

where ΣFournier is the sum of the categories of Fournier, divided by the maximum Fournier that can be reached by all individuals N in the sample.

The relationship of the meteorological and hydrological variables with the phenophases was evaluated using univariate Generalized Linear Models (GLMs) with quasi-binomial errors (Newbery et al. 2006; Dantas et al. 2016). We attribute 0 for absence and 1 for presence of phenophase, and the proportion of individuals manifesting certain phenophases in each month was calculated (Dantas et al. 2016).

Circular statistics was applied to verify whether the phenonological patterns of *P. macroloba* are seasonal (Morellato et al. 2010a). For this, the 12 months of the year were converted into angles, with intervals of 30°, from 0° = January (first month) to 330° = December (last month). The mean angle $\bar{a}$ and vector r parameters were calculated. The $\bar{a}$ indicates the period of year when phenophases are most frequently and the vector r is a measure of concentration around of the mean angle. The Rayleigh test (Z) was applied to assess the statistical significance of the mean angle and the following hypotheses were tested: H_0 = dates are randomly or uniformly distributed around the year and H_1 = dates are not uniformly distributed around the year. If the alternative hypothesis is accepted (H_1), the vector r can be considered a measure of the degree of phenological seasonality. The vector r has no unity and can vary from 0 to 1, greater is the phenological seasonality when the value approaches 1 (Morellato et al. 2000).

The Augspurger index of synchrony was calculated aiming to verify the presence or absence of synchrony in the flowering and fruiting phases (Augspurger 1983). The

Augspurger index of synchrony is calculated using the following formula:

$$X_i = \frac{\sum_n e_j}{(N-1)\cdot f_i}; Z = \frac{\sum X_i}{N}$$

where X_i is the synchrony index of individual i; Z is the population synchrony index; e_j is the number of months in which individuals i and j flourished synchronously, with $i \neq j$; f_i is the number of months that individual i flowered; N is the total number of individuals in the sample.

The intensity of the synchrony was classified in the following scales: 0—absence of synchrony; 0.1–0.27—minimum synchrony; 0.28–0.45—low synchrony; 0.46–0.69—medium synchrony; 0.70–0.99—high synchrony; and 1—perfect synchrony (Dantas et al. 2016). Basic commands of the R program were used to perform all statistical analysis (R core Team 2019), and the circular statistics was performed using the "circular" package (Agostinelli and Lund 2017).

Results

Hydrometeorology

The highest rainfall values were registered in the months of April 2018 (627 mm) and May 2019 (total rainfall 481 mm). The drought months were October 2018 (no rain) and September 2019 (total rainfall 2.8 mm). High mean maximum temperature always coincided with the month of October, reaching 34 ºC (Fig. 2a). The greatest amplitudes of flooding in the Amazon River (Fig. 2b) were recorded in the months of April 2018 (3.11 m height) and February 2019 (3.03 m height). When the rainfall in the region increases, the tide level of the Amazon River also increases ($r = 0.65$) and the temperature decreases ($r = -0.78$). There was a clear distinction between aquatic phase and terrestrial phase (Fig. 3, represented by bars) in the forest. Aquatic phase began in January and finished in July, influenced by increased rainfall ($r = 0.65$) and tide level of the Amazon River ($r = 0.56$). Terrestrial phase had duration of 5 months (August to December), when the volume of rainfall decreases and the maximum tidal amplitudes of the Amazon River were below 3 m.

Flowering

The flowering of the population of *P. macroloba* was annual and highly seasonal (flower bud: vector $r = 0.79$, $p < 0.001$; flowers in anthesis: vector $r = 0.81$, $p < 0.001$), with manifestation from July to December and with a mean duration of 3 months (±1 month). Production peaks of flower buds and flowers in anthesis occurred in September of 2018, with intensities of 27% and 28% in the population, respectively. In 2019, the peak of production occurred with less intensity, reaching 22% for both phenophases (Fig. 3a).

Most individuals (56%) showed medium synchrony with conspecifics in flowering and the rest (44%) showed high synchrony (Table 1). The population showed high synchrony in flowering ($Z = 0.70$).

The relationship was significant and positive between the maximum temperature with the flower bud ($\beta = 1.30$, SE = 0.36, $p < 0.01$) and anthesis flowers ($\beta = 1.84$, SE = 0.42, $p < 0.001$) phenophases (Fig. 4c; Table 2). With rainfall (Fig. 4a; Table 2), the correlations were negative and significant (flower buds: $\beta = -0.0088$, SE = 0.0031, $p < 0.01$; flowers in anthesis: $\beta = -0.011$, SE = 0.0035, $p < 0.01$). The relationships of the phenophases with the flood level were negative (Fig. 4b), but there was no statistical significance (Table 2).

Development of inflorescence and floral longevity

The first inflorescences appeared in the region of the apical bud of the branches, in the leaf petiole axilla. On the fourth day after the emission of the floral bud, it was possible to observe the distinction between peduncle and rachis of the inflorescence (Fig. 5, phase A). The rachis expands in size, more than the peduncle, gaining a light green color, confused with the color of the peduncle. On the twelfth day, the first flower buds appeared, showing a light green color (Fig. 5, phase B). On the eighteenth day, the rachis showed a dark green color and the flower buds expanded, forming the dividing lines of the sepal and petal structures. At this stage, the buds had a dark red color at the base of the calyx, light red at the transition between calyx and corolla and light green at the end of the petals (Fig. 5, phase C).

The development of flower buds had a mean duration of 15 days (±4 days). On the twenty-first day, the petals opened exposing the stamens that have the anther with light yellow color and white filament (Fig. 5, phase D). Then, several staminodes were exposed, giving the inflorescence a white color when viewed from a distance. Floral longevity (process of opening the petals until the senescence of the flower) had a mean duration of 2 days (±0.5 days), minimum 1 day and maximum 3 days, when the floral structures lose color and vigor (Fig. 5, phase E), generally at the end of the day.

Fruiting

Fruiting of *P. macroloba* was annual and highly seasonal (immature fruit: vector $r = 0.81$, $p < 0.001$; ripe fruit: vector $r = 0.71$, $p < 0.001$; seed dispersal: vector $r = 0.77$, $p < 0.001$) manifesting from September to June, with a mean duration of 5 months (±3 months). All the immature fruit peaks occurred in November (Fig. 3b), with 33% intensity

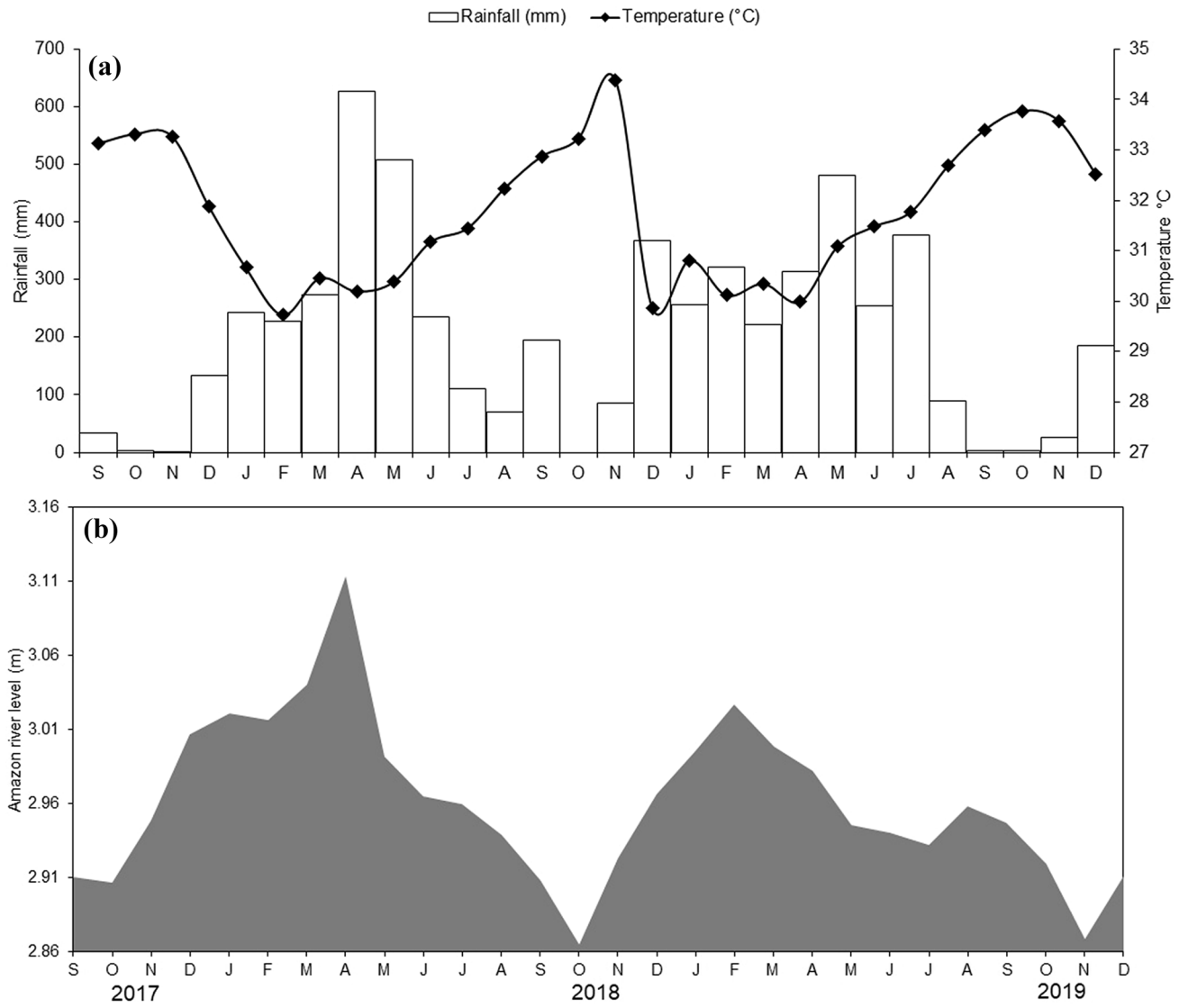

Fig. 2 Rainfall (empty rectangle), mean maximum temperature (continuous line with diamond) and mean tidal amplitude of the Amazon River (filled square) in the floodplain forest of the Amazon estuary, Macapá, Brazil. Source: **a** INMET—National Institute of Meteorology; **b** Brazilian Navy Hydrography Center (Marinha do Brasil)

in 2017, 35% in 2018 and 25% in 2019. Production peaks of ripe fruits occurred in January/2018 (31% intensity) and in February/2019 (37% intensity). Seed dispersal peaks occurred in March 2018 (31% intensity) and in April 2019 (23% intensity).

Most individuals showed medium fruiting synchrony (88%) and the rest of the trees (12%) showed high synchrony (Table 1). The population showed medium synchrony for fruiting $Z = 0.61$.

The correlations of the immature fruit phenophase with the rainfall ($\beta = -0.0056$, SE = 0.0025, $p < 0.01$, Fig. 4d) and water level ($\beta = 0.13$, SE = 0.51, $p < 0.01$, Fig. 4e) were negative and significant (Table 2). With maximum temperature, the correlation was positive and significant ($\beta = 0.67$, SE = 0.30, $p < 0.01$, Fig. 4f). Ripe fruit was positively correlated with the water level ($\beta = 0.05$, SE = 0.019, $p < 0.05$, Fig. 4e). Seed dispersal was positively and significantly correlated with rainfall ($\beta = 0.0051$, SE = 0.0021, $p < 0.01$, Fig. 4d) and water level ($\beta = 0.12$, SE = 0.02, $p < 0.001$, Fig. 4e).

Leaf change

Leaf emission and leaf fall occurred continuously throughout the year and not showed seasonality (new leaves: vector $r = 0.07$, $p > 0.05$; leaf fall: vector $r = 0.05$, $p > 0.05$). There was no clear peak of intensity of the phenophases. *P. macroloba* remains with the canopy evergreen, at the same time,

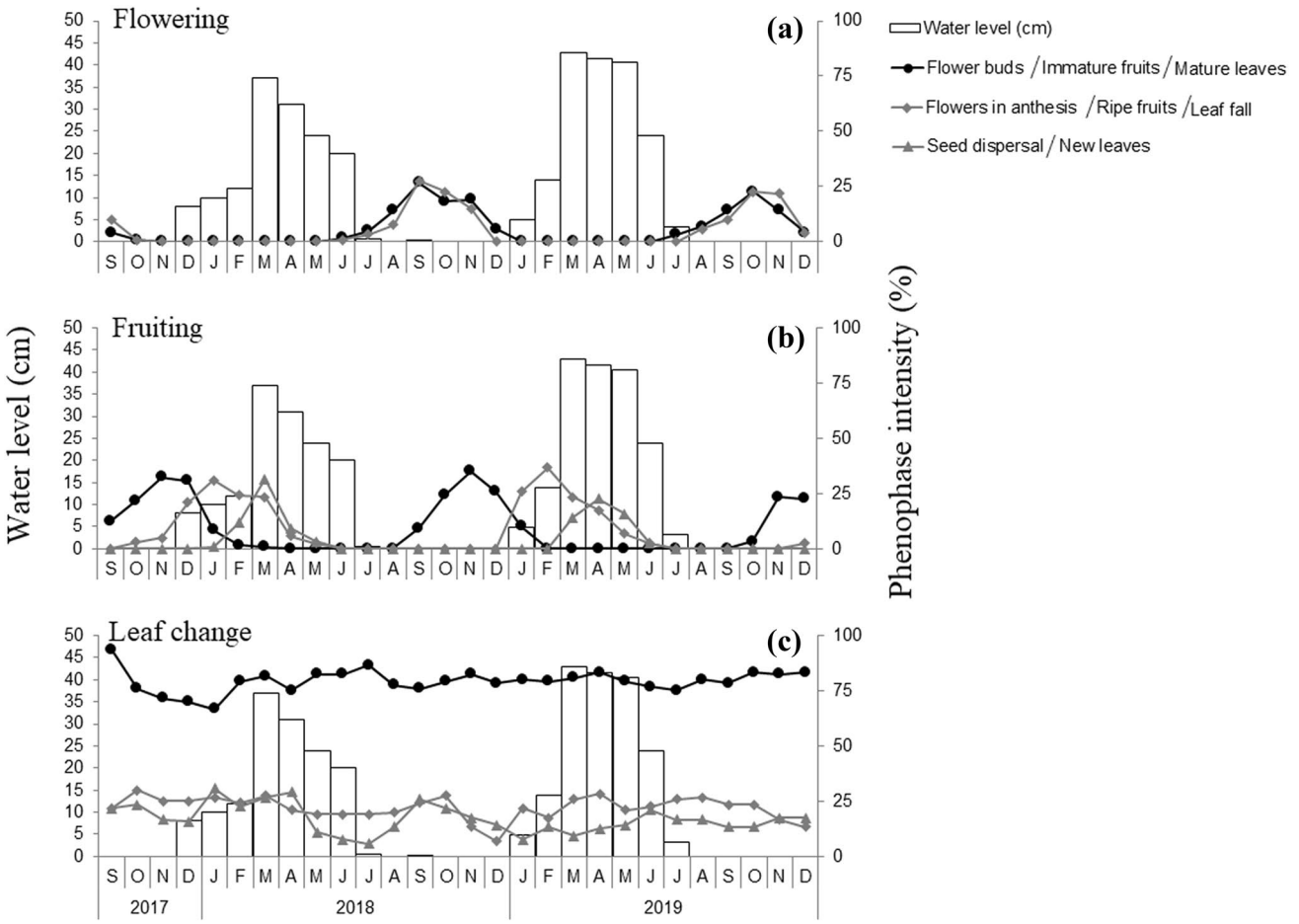

Fig. 3 Intensity of the phenophases of *Pentaclethra macroloba*, in relation to the water level in the floodplain forest of the Amazon estuary, Macapá, Brazil

producing new leaves (Fig. 3c). There was no significant correlation between phenophases and the tested hydrometeorological variables (Table 2).

Description of the activity and behavior of floral visitors

Monitoring the activity of floral visitors resulted in 31 field days and 100 h of observation. During field monitoring, wasps, bees and ants were frequently seen foraging the inflorescence of *P. macroloba* (Table 3). Beetles also appeared frequently to feed of the flowers (video beetle-flower interactions, Supplementary 2).

The wasps, always in number of 12–42 individuals, flew over the inflorescence in search of a gap between the numerous staminodes. When an opening was located, the wasps landed on the staminodes and went towards the corolla of the flower (where the stamens and ovary are located) and remained there for 5–7 min foraging and vibrating the hind legs (video wasp-flower interactions, Supplementary 3). Bees explored the flowers in small groups of individuals, from three to five insects, and always flew in circles around the inflorescence to reach the interior of the flower. The bees remained inside the flower for 8–11 min and they alternated between several flowers at the same time. Bees were seen foraging flower buds, in addition to flowers, together with the ants (video bee-ant-flower interactions, supplementary 4).

Wasps frequently visited the flowers between the hours of 12:00 and 14:00 pm, with peak visitation at 12:00 am (Fig. 6a). The preferred time of the bees occurred between 08:00 and 12:30 pm, with peak visitation at 10:00 am (Fig. 6b). Ants had a wider visitation time, but the peak visitation occurred at 11:00 am (Fig. 6c). When the wasps identified other intruder insects trying to exploit an inflorescence dominated by the group, they exhibited aggressive behavior and went to attack the intruders with their stingers. This behavior may justify the low number of species that visited the inflorescence of *P. macroloba* (Table 3).

Table 1 Synchrony index of flowering and fruiting for the individual (Xi) and for the population (Z) of *Pentaclethra macroloba* in the floodplain forest of the Amazon estuary, Macapá, Brazil

Trees	Flowering (Xi)	Intensity	Fruiting (Xi)	Intensity
px133	0.68	Medium	0.65	Medium
px143	****	****	****	****
px158	0.81	High	0.70	High
px160	0.54	Medium	0.53	Medium
px161	****	****	****	****
px162	0.65	Medium	0.64	Medium
px258	0.68	Medium	0.67	Medium
px165	0.75	High	0.53	medium
px422	0.67	Medium	0.75	high
px171	0.64	Medium	0.62	Medium
px17	0.63	Medium	0.58	Medium
px80	0.63	Medium	0.67	Medium
px89	****	****	****	****
px144	0.62	Medium	0.61	Medium
px154	0.72	High	0.60	Medium
px264	0.72	High	0.64	Medium
px163	****	****	****	****
px401	0.67	Medium	0.62	Medium
px921	0.72	High	0.51	Medium
px911	0.72	High	0.55	Medium
px947	0.68	Medium	0.58	Medium
px1132	0.79	High	0.50	Medium
px1149	0.75	High	0.64	Medium
px1152	0.78	High	0.75	High
px1640	0.78	High	0.58	Medium
px1583	0.75	High	0.54	Medium
px1589	0.65	Medium	0.58	Medium
px1805	0.68	Medium	0.58	Medium
px765	0.68	Medium	0.58	Medium
Population (Z)	0.70	High	0.61	Medium

*****Did not flower during the study period

Discussion

Flowering in the dry season seems to be common in the Amazonian estuary. In the same area of this study, Dantas et al. (2016) found flowering peaks from September to October for the multi-uses, seeds produces medicinal oil, species *Carapa guianensis* Aubl. (Meliaceae). In Combu Island, estuary in Pará State, trees also emit more flowers during the driest months of the year, from July to December (Cattanio et al. 2004). The flowering period of *P. macroloba* differs from the trees of flooded forests in the Central Amazon. Some trees produce flowers at the beginning of the flood period (Worbes 1997) and others at the peak of the river flood (Schöngart et al. 2002). However, Haugaasen and Peres (2005) studied the phenology of arboreal communities in the *várzea* and *igapó* forests of the lower Purus River, west of the Central Amazon, and found that species from both environments showed marked flowering peaks during the dry season, from July to October.

Flower production in the dry season, where temperatures are high and the rainfall is low, becomes a reproductive trigger for *Pentaclethra macroloba*. The intense rains of the rainy season in the Amazon can damage the floral structure, affecting pollen viability and stigma receptivity (Dantas et al. 2016). For floral visitors of *P. macroloba*, such as wasps and bees, the dry season is ideal for foraging flowers, because rain interferes with the pollination activity of the insects. In a broad review of the effects of rainfall on pollinator–plant interactions, Lawson and Rands (2019) found that rainfall causes mechanical restrictions on the insect wings and interferes with their sensory signals. In general, rainfall can cause various effects on insects and other arthropods, which can seriously damage trophic interactions (Chen et al. 2019).

P. macroloba population showed highly synchronized flowering between individuals. Synchronized flowering favors cross-pollination (Nilsson and Wästljung 1987; Stevenson et al. 2008; Narbona et al. 2011), as pollinators can forage several individuals during the day, while mixing and transferring pollen from neighboring trees (Augspurger 1981; Braga and Collevatti 2011). The low flowering intensity of *P. macroloba*, between 23 and 25%, indicates that the species does not show mass-flowering, in which the tree produces a large number of flowers at once (Augspurger 1980). Although the population of *P. macroloba* shows synchronism in flowering, the branches of the tree making flowering are not synchronized. When one branches is in floral senescence, another is already bearing new inflorescences, ensuring continuous production and of low intensity during the flowering period.

Synchronized flowering, however, can also be a disadvantage for trees, due to attract the attention of predators (Rathcke and Lacey 1985). During the flowering period of *P. macroloba*, it was common to observe undeveloped inflorescences on the forest floor. This is probably due to the presence of predators, such as beetles found in inflorescences. For Kevan and Baker (1983), beetles are common in trees with synchronized flowering, as they feed of the plant sap and floral structures. However, several other factors can contribute to flower abortion (Stephenson 1981; Bawa and Webb 1984), such as water deficiency (Rapoport et al. 2012). This factor could affect more directly the development of *P. macroloba* inflorescence, since its flowering is concentrated in the dry season.

The period that trees remain with its flowers open is an important aspect to understand the plant–pollinator interactions (Primack 1985). The floral development of *P. macroloba* can last up to 20 days and anthesis three days. This

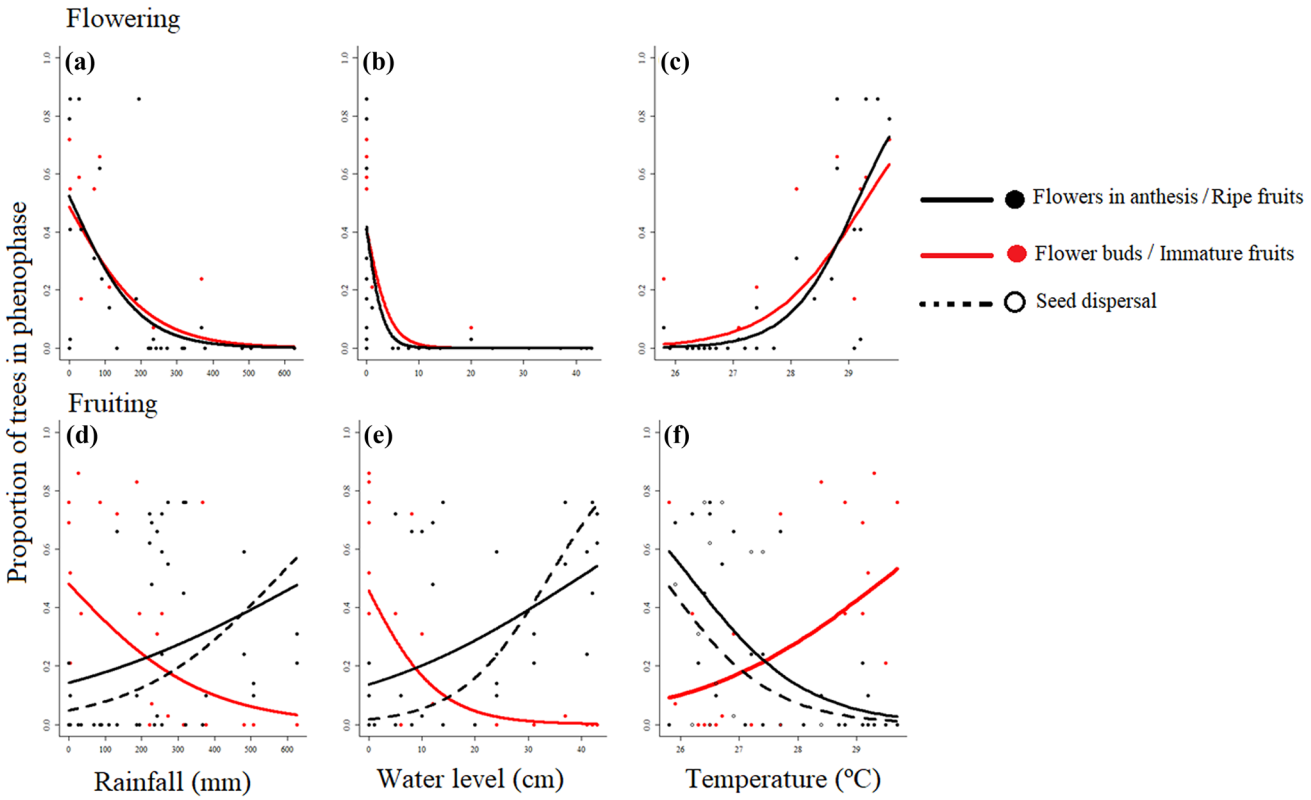

Fig. 4 Relationship between the proportion of individuals of *Pentaclethra macroloba* in phenophase with the hydrometeorological variables in the floodplain forest of the Amazon estuary, Macapá, Brazil

Table 2 Magnitude of the effect (β) of the variables of rainfall (R), water level (WL) and temperature (T) in the proportion of *Pentaclethra macroloba* individuals in phenophases in the floodplain forest of the Amazon estuary, Macapá, Brazil (based on GLMs with quasi-binomial errors)

Phenophases	β_R	SE_R	B_{WL}	SE_{WL}	β_T	SE_T
Flower bud	− 0.0088**	0.0029	− 0.40^{ns}	0.33	1.25**	0.36
Flower in anthesis	− 0.011**	0.0039	− 0.56^{ns}	1.19	1.74***	0.40
Immature fruit	− 0.0053*	0.0024	− 0.14*	0.052	0.62*	0.29
Ripe fruit	0.0027^{ns}	0.0017	0.05*	0.019	− 1.02**	0.28
Seed dispersal	0.0052*	0.0022	0.12***	0.02	− 1.11**	0.39
New leaf	0.0001^{ns}	0.0008	− 0.006^{ns}	0.009	0.11^{ns}	0.11
Mature leaf	NT	NT	NT	NT	NT	NT
Leaf fall	− 0.001^{ns}	0.001	0.012^{ns}	0.012	0.23^{ns}	0.01

SE standard error, *NT* not tested, *significant at 0.05, **significant at 0.01, ***significant at 0.001 and ^{ns}not significant

cost can be rewarded, in trees with low floral longevity such as *P. macroloba*, for a high frequency of pollinators (Spigler 2017), no being necessary an extended anthesis for several days, which avoids geitonogamy and the displacement of nutritional energy for the flower.

The behavior shown by wasps and bees when foraging the flower, lead to the assumption that they are legitimate pollinators of *P. macroloba*. At the La Selva Biological Station in Costa Rica, Bawa et al. (1985) found small bees pollinating *P. macroloba*. These little Hymenoptera are attracted by the sweet smell that the flowers release (personal observation). The nectar guides present on the petals (Dantas et al. 2021) attract insects towards the nectar gland at the base of the ovary (Barros et al. 2017). This increases the chances of the reproductive organs of the flower being touched by the movement of the insect when they enter the corolla.

Ants were also frequently observed foraging the flower buds of *P. macroloba*. Perhaps, the ants are attracted by the extrafloral gland present at the base of the *P. macroloba* leaf (Dantas et al. 2021). Extrafloral nectar is rich

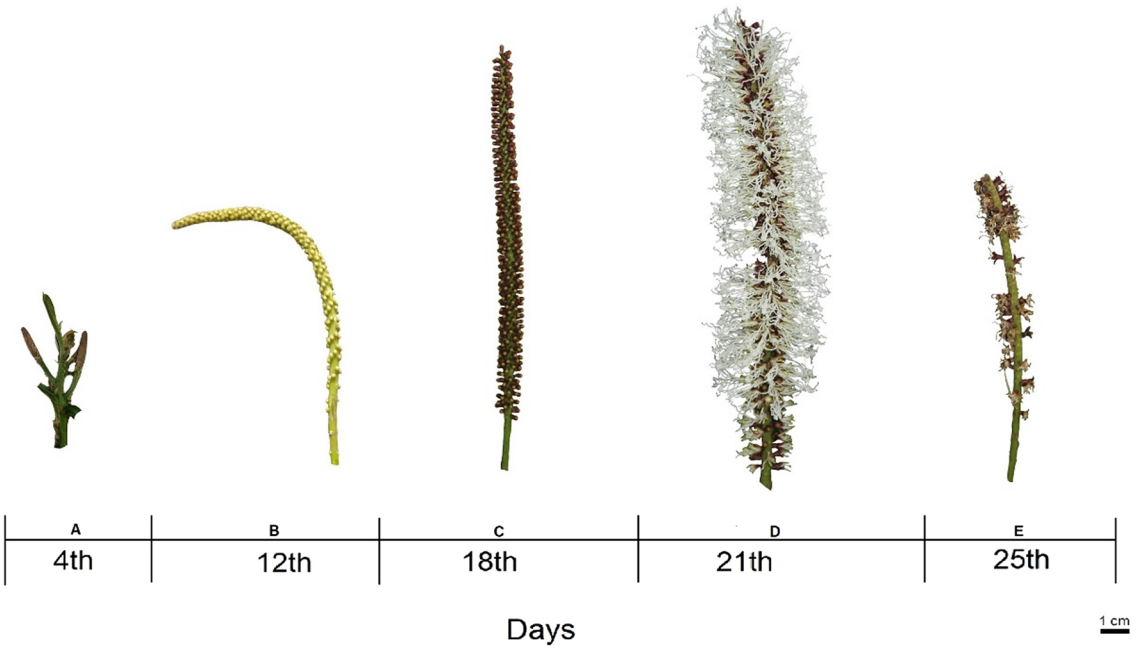

Fig. 5 Development of inflorescence and floral longevity of *Pentaclethra macroloba* in the floodplain forest of the Amazon estuary, Macapá, Brazil: Phase A: formation of peduncle and rachis of the inflorescence; Phase B: Appearance of the first flower buds; Phase C: expansion and maturation of flower buds; Phase D: Floral anthesis; and Phase E: floral senescence

in carbohydrates and amino acids, essential energy source for canopy ants (Byk and Del-Claro 2011). Ants of the species *Paraponera clavata* (Fabricius, 1775) have mutualistic interactions with individuals of *P. macroloba* from Central America. The tree offers extrafloral nectary and shelter for the ant and the ant rewards protecting the plant of the herbivores (Bennett and Breed 1985).

Other studies also show the predominance of species fruiting and dispersing propagules at the peak of flooding in the forest, both in Central Amazonia (Worbes 1997; Schöngart et al. 2002; Haugaasen and Peres 2005; Ferreira and Parolin 2007; Hawes and Peres 2016) and in the Amazon estuary (Cattanio et al. 2004; Dantas et al. 2016). This shows that the flood pulse is an important driver of the phenological patterns of the Amazon flooded forests.

Fruiting of *P. macroloba* was influenced by the increased of the rainfall and water level inside the forest. In floodplain forest, the flood pulse and rainfall act as synchronizers of the phenological rhythms of many species, mainly in the stage of ripening of the fruits (Parolin et al. 2010). This period is ideal for species to disperse their propagules, because many trees depend of the ichthyofauna (Kubitzki and Ziburski 1994) and river water to transport their seeds (Moegenburg 2002; Cunha et al. 2017).

The ripening time of the fruits reflects on the successful dispersion of the seeds (Rathcke and Lacey 1985). The high temperatures that the fruits receive during the development in the dry season, favor the maturation and desiccation of the fruits, which is essential for the release of the seeds when the fruits are ripe in the rainy season. According to van Rheede van Oudtshoorn and van Rooyen (1999), Fabaceae trees which release their seeds by the explosive dehiscence of the fruits, need water for the cells of the dry tissue of the fruits to absorb the liquid and cause tension in the valves. As a result, the valves twist in the abscission zone of the fruit and expel the seeds away from the tree. In the case of *P. macroloba*, the seeds can be expelled up to 10 m (Hartshorn 1983).

Table 3 Floral visitors of *Pentaclethra macroloba* in the floodplain forest of the Amazon estuary, Macapá, Brazil

Species	Visitors (N)
Ant	
Paraponera clavata (Fabricius, 1775)	26
Beetle	
Palidonata sp.	3
Bees	
Trigona fulviventris (Guérin, 1985)	18
Trigona sp1	7
Trigona sp2	9
Melipona sp.	5
Wasps	
Mischocyttarus alfkenii (Ducke, 1904)	42
Mischocyttarus sp.	31

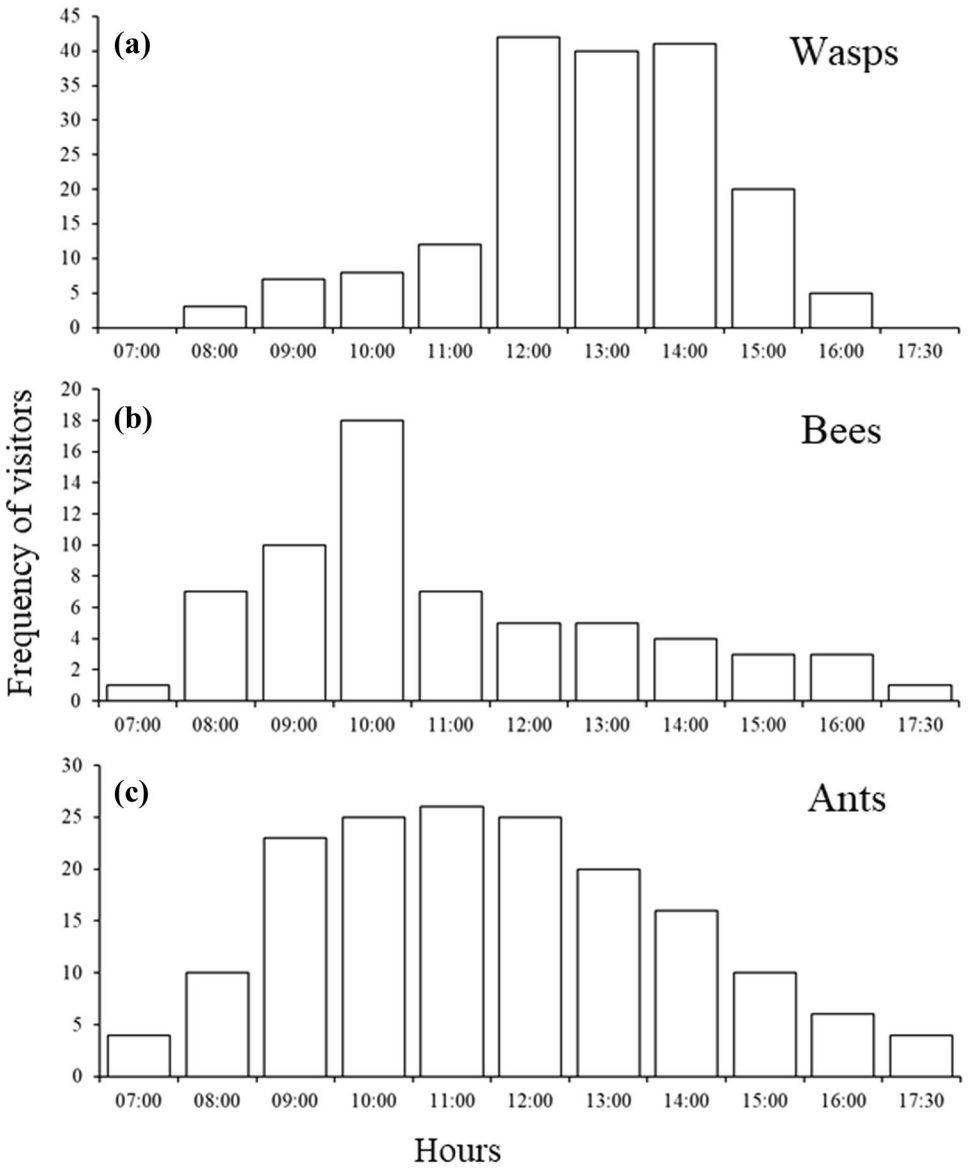

Fig. 6 Foraging activity of the main floral visitors, between the hours of 07:00 and 17:30, during 31 days of observation in *Pentaclethra macroloba* in the floodplain forest of the Amazon estuary, Macapá, Brazil

The synchrony of the seed dispersal with the rainy season and flood peak of the Amazon River, allows *P. macroloba* to disperse its seeds over a long distance by hydrochoria (Williamson and Costa 2000). The flattened shape (deltoid) and the accumulation of air between the cotyledons, allow the seed to glide when leaving the fruit, and float when reaching the water of the Amazon estuary obtaining greater efficiency in dispersion (Dantas et al. 2021). Correa et al. (2018) suggest that the synchronization of fruiting time with the flooding peak contributed to the evolution of the patterns of hydrochoric and ichthyochoric dispersion found in the flooded forests of the Amazon. The authors emphasize that these two types of dispersion also directed the phenological behavior of the trees, so that they respond presenting more attractive and fleshy fruits for the fish and mechanisms adapted to buoyancy in water.

P. macroloba remains evergreen while unfolding and losing leaves, and there is no clear relationship with the hydrometeorological variables. The characteristic of presenting always ripe leaves and continuous production of new leaves, can decrease the herbivory rate of flowers and fruits. Many leaves in the canopy can block and hide the reproductive elements from the view of herbivores. In addition, Klimas et al. (2012) suggest that the continuous production of leaves increases the photosynthetic area of the canopy, allowing the species to stock higher amounts of carbohydrates in the leaves to use in the reproductive phase.

Conclusions

The high degree of synchrony of the reproductive phenophases with the seasons of the year, suggests that *P. macroloba* has high adaptation and reproductive strategies in the tidal floodplains of the Amazon estuary, this may be one of the factors that explain its dominance in this environment.

The seasonality of the rainy season has a major influence on the reproductive phenology of *P. macroloba*. The decrease in rainfall from September to December causes an increase in air temperature, which is essential to stimulate the flowering and the production of the first fruits. The increase in rainfall favors fruit ripening and triggers their explosive dehiscence mechanism. The flood pulse of the Amazon River may be a synchronizing agent in the *P. macroloba* seed dispersal phenophase, this environmental drive is essential for the transport of seeds and colonization of other areas.

Our results will be fundamental to assist in the good practices of *P. macroloba* seed management and in the valuation of non-wood forest products in estuarine floodplain forests.

Author contribution statement ARD, MCG, ACLG and MTFP conceived the ideas and designed methodology; ARD collected the data; ARD, MCG, ACLG and MTFP analyzed the data; ARD led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Compliance with ethical standards

Conflict of interest The authors declare that there is no any conflict of interest.

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